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PRELIMINARY STUDIES IN THE GENUS DENTARIA IN EASTERN NORTH AMERICA*

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THE taxonomy of the eastern North American species of the genus *Dentaria* (Cruciferae) has been a problem to botanists for many years. So closely may characteristics of some specimens in one species resemble those of another species, that the task of separating them seems hopeless. Considering the two most widely distributed species, Wiegand and Eames (1926) remarked "Many plants of *Dentaria* differ in various ways from typical *D. diphylla* and *D. laciniata*. These have been a constant source of difficulty to local botanists. Field studies through many seasons have led the authors to the belief that these plants are all of hybrid origin, with *D. diphylla* and *D. laciniata* as parents."

Coulter, as far back as 1875, suggested, "These several species (*D. maxima*, *heterophylla*, *laciniata*, and *multifida*) should certainly be reduced to one, and some such name as *D. heterophylla* be given to it." Indeed, had he been aware of the variability of *D. diphylla*, he might well have included it with the other species.

The fact that hybrids between nearly all species have been suggested also gives an indication of the complex taxonomic status of the species. Haberer and House (1923) described three hybrids, *D. diphylla* × *maxima* Haberer, *D. laciniata* × *maxima* Haberer, and *D. laciniata* × *diphylla* House. The second hybrid was considered to be similar to *D. incisifolia* Eames, and the third to correspond to *D. anomala* Eames. Dr. E. Lucy Braun on herbarium specimens and in personal correspondence has suggested the hybrids *D. laciniata* × *heterophylla*, and *D. multifida* × *heterophylla*. The presence of the parent species in the areas where the hybrids were found, as well as appearances, was the basis for her determinations.

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Up to the present, the differentiation of species and hybrids has been based chiefly on morphology. The data presented in this paper are based not only on a morphological study of specimens from numerous herbaria and in the field, but also include information obtained from cytological, embryological, pollen and fertilization studies.

MATERIALS AND METHODS

Herbarium material was examined from the following sources:

Dr. E. Lucy Braun (private collection), Cincinnati, Ohio; Clemson College, Clemson, S. C.; Chicago Museum of Natural History, Chicago, Ill.; Cornell University, Ithaca, N. Y.; Division of Botany and Plant Pathology, Ottawa, Ont.; Gray Herbarium, Harvard University, Cambridge Mass.; McMaster University, Hamilton, Ont.; Montreal Botanic Garden, Montreal, Que.; Missouri Botanical Garden, St. Louis, Mo.; National Herbarium, Washington, D. C.; National Museum of Canada, Ottawa, Ont.; New York Botanical Garden, New York, N. Y.; North Carolina State College, Raleigh, N. C.; University of Cincinnati, Cincinnati, Ohio; University of Georgia, Athens, Ga.; University of Iowa, Ames, Iowa; University of Michigan, Ann Arbor, Mich.; University of North Carolina, Chapel Hill, N. C.; University of Tennessee, Nashville, Tenn.; University of Toronto, Toronto, Ont.; University of Wisconsin, Madison, Wisc.; University of Western Ontario, London, Ont.

Rhizomes were collected by the writer from Ontario, and the states of Alabama, Georgia, New York, Tennessee, and Virginia. Dr. Wilbur H. Duncan of the University of Georgia very kindly contributed further materials from Alabama and Georgia. Root-tips from these rhizomes were fixed in acetic-alcohol, 1:3, stained by the Feulgen technique, mounted in aceto-carmine and squashed under the coverslip. Chromosome counts and photographs were made before the slides were made permanent.

Pollen for determining the percentage of mature pollen grains was obtained for all species, and from areas throughout the range of each species. Following the technique of Downs (1943), pollen was mounted in polyvinyl alcohol. To give a stain so that the pollen grains could be more easily seen, we dissolved acid fuchsin in the mounting medium. Mature pollen grains stained a deep pink; aborted or empty grains did not take the stain.

TAXONOMIC NOTES

O. E. Schulz (1903) monographed the genus *Cardamine,* and in his monograph considered the genus *Dentaria* to be a section of *Cardamine.* The combining of the two genera was not without precedent, for Crantz (1769), Robert Brown (1812), and Wood (1870) listed the species of *Dentaria* under *Cardamine.* Recent floras in America, as well as in Europe, however, have continued to separate the two genera. Until both have been studied more completely by modern taxonomical methods, no conclusive evidence as to the relationship between them can be established.

The first species of *Dentaria* to be described in eastern North America was *D. laciniata* by Willdenow (1800), apparently from letters and collections sent to him by Muhlenberg. The main diagnostic characteristic was the three, three-parted leaves. In 1803, Michaux described as *D. concatenata,* a species having tuberous segments united by a narrow connective, and with three, three-parted leaves. This has been made synonymous with *D. laciniata.* This leaf character and the concatenate root-stocks are still accepted as the outstanding features of the species. The rhizomal leaf (if present) and the flowering stem arise from the end of the rhizome segment of the previous year. The involucral leaves may be two instead of the typical three. They may be glabrous or pubescent. The peduncles and pedicels most frequently do have pubescence. The trichomes are comparatively long and more or less perpendicular to the leaf, peduncle and pedicel surface. In this respect, they resemble the trichomes of *D. maxima.*

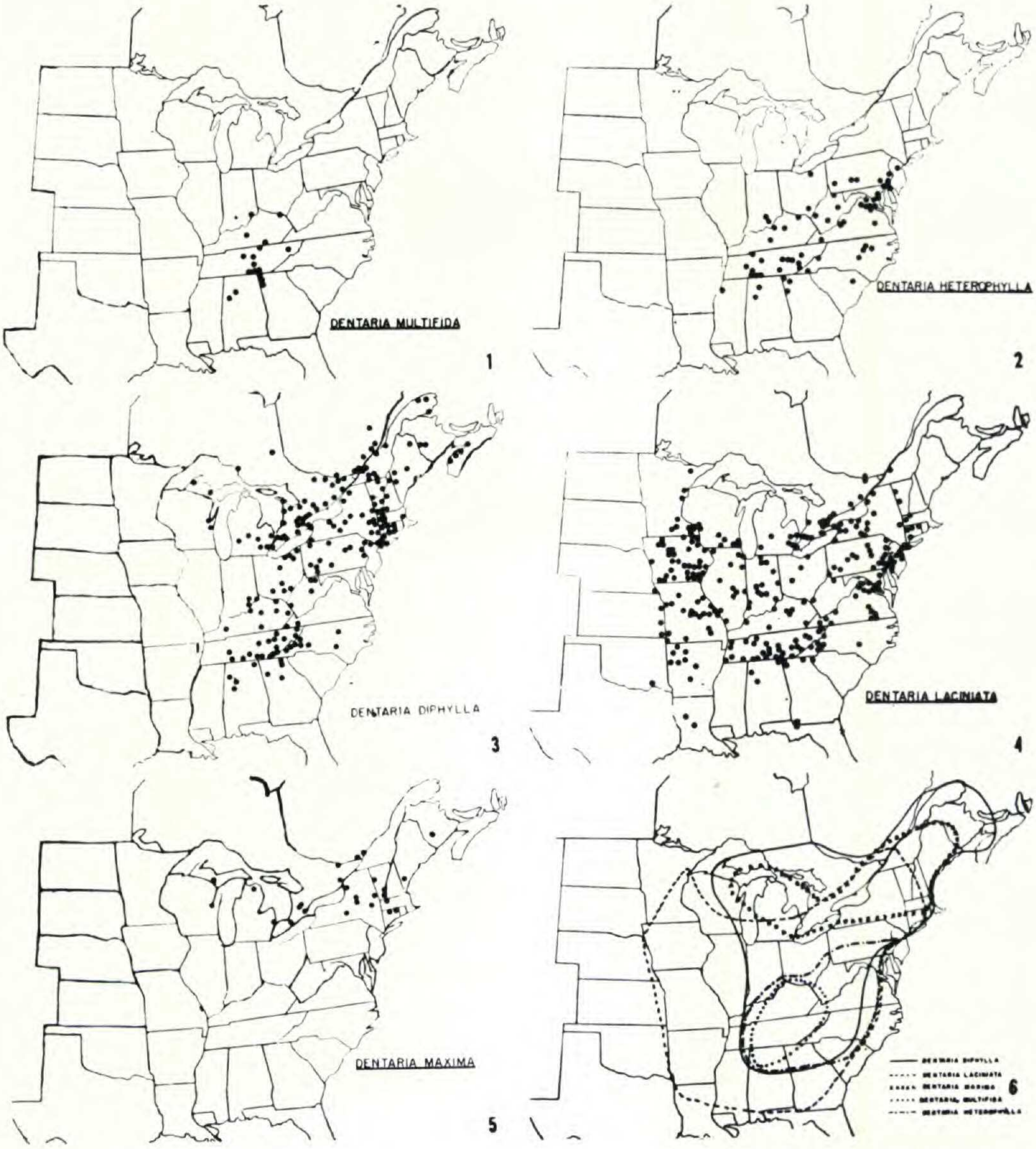
Although all species are polymorphic, in no other has varieties been described. When the leaves are two, they may be opposite, var. *opposita* Farwell (1931). Typically the leaves are in whorls but they may be alternate as in var. *alterna* Farwell (l.c.). As in the original description the leaflets are basically three-parted, but the lateral leaflets may be again divided, giving a five-parted appearance. Several varietal names have been given to variations in those specimens having simply three-parted leaflets, e.g. var. *furcata* Small, (1903), var. *integra* (O. E. Schulz) Fernald, (1908), var. *latifolia* Farwell (l.c.). Variety *coalescens* Fern. (1938) has the leaves merely three-cleft or pinnatifid. Schulz (1903) described a variety with the pubescence also covering the silique, var. *lasiocarpa*.

Dentaria laciniata has a wide distribution (fig. 4). It extends farther westward and southward than any other species, but no records have been seen for Maine and the Maritime Provinces of Canada. Only in southern Ontario has it been found north of the Great Lakes.

Michaux (1803) described *D. diphylla* as the *Dentaria* with dentate roots, with two stem-leaves approximate and three-parted. The rather stout, continuous, dentate rhizomes, on or close to the surface of the ground, are the best distinguishing feature of the species. The basal or rhizome-leaf, and the flowering stem arise from the same point at the end of the rhizome, but the new underground growth forms so quickly in the spring that these may appear to originate from the surface of the rhizome. In all other species the above ground parts appear to come from the constricted portion of the rhizome—actually the tip of the former year's growth. The two, three, or more involucral leaves may be opposite, sub-opposite, or alternate. These leaves are three-parted. The very short, forward-pointing trichomes on the margins of the leaflets may be used to distinguish this species from *D. laciniata, maxima* and *multifida;* however, *D. heterophylla* has similar marginal trichomes. The peduncles and pedicels are nearly always glabrous. The number, size, and color of the flowers varies considerably, and no constant character has been noted.

Dentaria diphylla covers most of the range of the genus (fig. 3) but does not extend as far west as *D. laciniata*. It is, however, found farther northward and eastward than *D. laciniata*.

Dentaria multifida was catalogued by Muhlenberg (1813) but was first described by Nuttall (1818). It is the most delicate of our species. It has very small, concatenate rhizomes with the segments rather firmly united. The leaves are basically similar to *D. laciniata*, being three-parted. The primary divisions are further divided into linear segments. For this reason



Distribution of Eastern North American Species of Dentaria. Fig. 1. *D. multifida;* Fig. 2. *D. heterophylla;* Fig. 3. *D. diphylla;* Fig. 4. *D. laciniata;* Fig. 5. *D. maxima;* Fig. 6. Composite map of distribution areas.

Leavenworth (1824) described *D. dissecta* from a specimen from Cherokee Co., Tenn. This has been placed in synonymy. No pubescent specimens have been seen. Some specimens of *D. multifida* may approach *D. laciniata* in appearance, and vice-versa. Schulz (l.c.) treated *D. multifida* as a variety of *D. laciniata* and said that it was bound with the main species through a continuous series of intermediates.

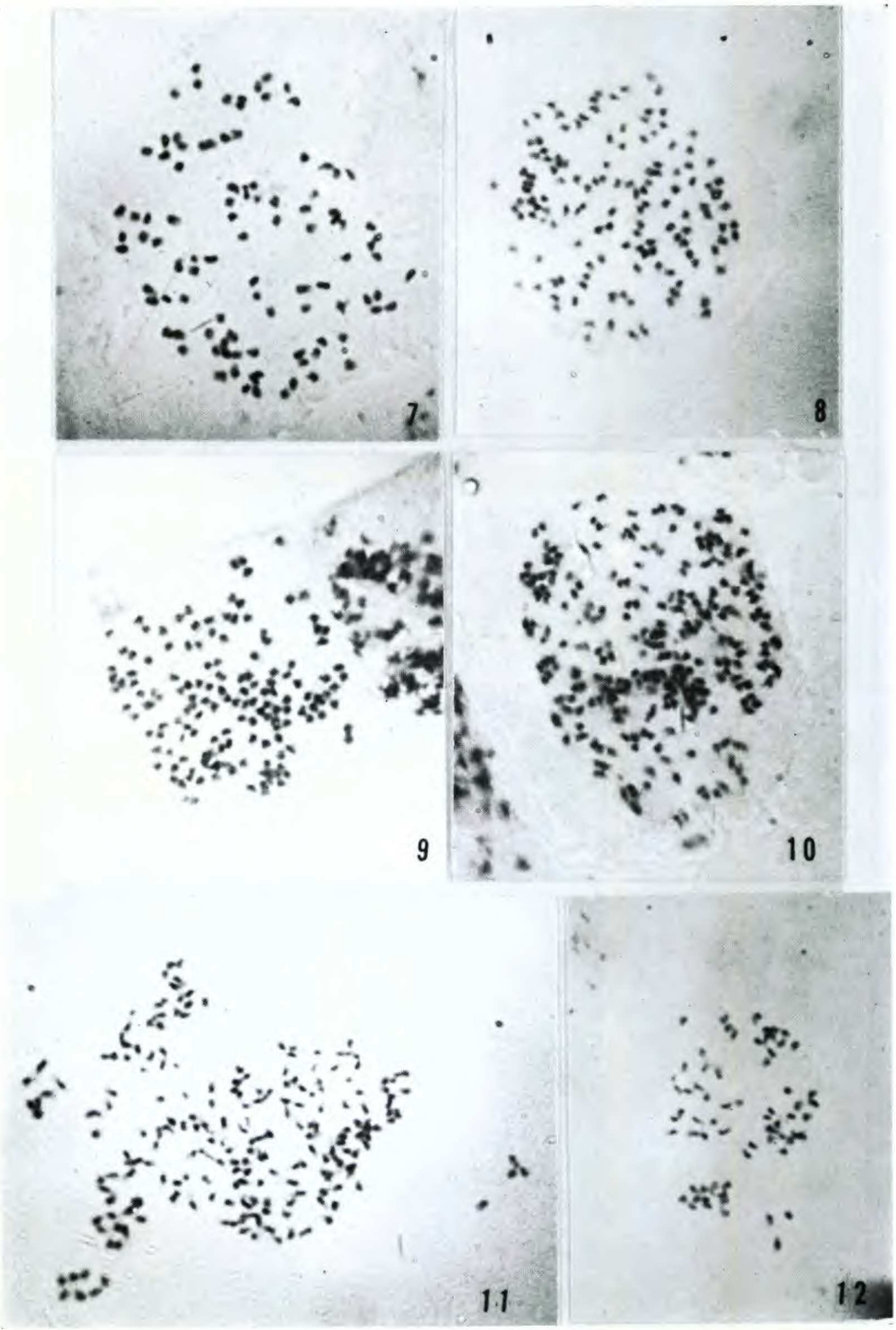
D. multifida has a restricted distribution (fig. 1). Its area of greatest frequency is Tennessee, northern Georgia and northern Alabama.

Nuttall's description of *D. heterophylla* (1818) might well apply to *D. diphylla,* except for the concatenate rhizome. In *D. heterophylla* the segments are short, slender and rather firmly united by a narrow connective. The size of the segments distinguishes them from those of *D. laciniata.* In examining specimens it was frequently necessary to observe the rhizomes in order to separate *D. heterophylla* and *D. diphylla.*

The area of *D. heterophylla* (fig. 2) is much more restricted than that of *diphylla* and *laciniata,* but wider than that of *multifida.* It has migrated into southern Indiana, Ohio and Pennsylvania.

Dentaria maxima was rather thoroughly described by Nuttall (l.c.). His description of the rhizomes requires some clarification. Nuttall described them as "concatenate" but this would not distinguish them from those of *D. laciniata, D. heterophylla* and *D. multifida.* The rhizomes of *Dentaria maxima* closely resemble those of *D. diphylla,* but are distinguished by alternately enlarged and only slightly constricted regions. Also, as to the size and number of leaves and leaflets, the specimens that Nuttall described must have been rather singular. "Stem often near 2 ft. high,—leaves 5 to 7." In the specimens examined, stems seldom exceeded 1 ft. in height, and most frequently there were 3 alternate leaves. However specimens with one, two, or several leaves are to be found. The leaflets are usually more sharply toothed than those of *D. diphylla.* The leaf characters vary, and in some areas they approach those of *diphylla.* In other localities, e.g. Taughannock Falls and Enfield Glen, New York, and Milton and Kitchener, Ontario, the leaves are difficult to distinguish from those of *laciniata.* Nuttall mentioned the slightly asperate margin of the leaf. The trichomes there were found to be longer and more nearly perpendicular to the margin of the leaf than the trichomes of *diphylla.* They are superficially similar to those of *laciniata.* The peduncles are most frequently glabrous, but pubescent specimens have been seen.

D. maxima occurs entirely within the area of the Wisconsin glaciation (fig. 5), and its main distribution is in New York State, and the Provinces of Ontario and Quebec.



Chromosomes of Dentaria Species (× 2000). Fig. 7. *D. diphylla*, $2n = 96$; Fig. 8. *D. multifida*, $2n = \pm 112$; Fig. 9. *D. heterophylla*, $2n = \pm 128$; Fig. 10. *D. laciniata*, $2n = \pm 240$; Fig. 11. *D. maxima*, $2n = \pm 208$; Fig. 12. *D. multifida* from Rome, Ga., $2n = 64$.

CYTOLOGY

The chromosomes in all species are small and numerous. This latter fact made it difficult always to obtain complete separation of the chromosomes. Their size prohibited a study of chromosome morphology, but most of them seemed to have a median centromere. Some had a sub-terminal centromere which was rather elongated and often made it uncertain whether one should count one or two chromosomes.

Table 1 gives the chromosome numbers for the species studied.

TABLE 1. CHROMOSOME NUMBERS FOR EASTERN NORTH AMERICAN SPECIES OF DENTARIA

Species	*Source of material*	*No. of cell counts*	*2n no.*
D. diphylla (Fig. 7)	Kitchener, Guelph, Ont.	21	96
D. heterophylla (Fig. 9)	Markham, Va.; Rome, Ga.; Winston Co. Ala.; Johnston City, Tenn.;	42	±128
D. laciniata (Fig. 10)	Kitchener, Guelph, Ont.	15	±240
D. maxima (Fig. 11)	Guelph, Milton, Ont.; Enfield Glen, N. Y.; Taughannock Falls, N. Y.	15	±208
D. multifida (Fig. 8)	Vilanow, Ga.; Chattanooga, Tenn.	10	±112
(Fig. 12)	Rome, Ga.	5	64

Chromosome studies by other workers have shown that most species of *Dentaria* studied from other parts of the world are also polyploids. Those species for which chromosome counts have been made are as follows:

TABLE 2. CHROMOSOME NUMBERS OF SPECIES OUTSIDE OF EASTERN NORTH AMERICA

Species	*2n Chromosome No.*	*Author*
D. polyphylla	48	Schwarzenbach, 1922
D. pentaphylla	48	Schwarzenbach, 1922
D. pinnata	48	Schwarzenbach, 1922
D. bulbifera	ca 96	Manton, 1932
D. californica	32	Manton, 1932
D. savensis	ca 80	Manton, 1932
D. macrophylla	16	Morinaga & Fukushima, 1931

With the exception of *D. californica* these are European and Asiatic species.

The basic chromosome number has been given as x = 8 by Darlington and Janaki Ammal (1945). This number is certainly basic to the American species studied here, but the 2n number exceeds those found so far in other parts of the world.

It is the writer's opinion that the chromosome numbers given in Table 1 are not all that may be obtained for specimens in our area. The fact that one specimen of *D. multifida* from Rome, Ga., had 2n = 64 would give credence to this opinion; also the origin of our present species would indicate that other chromosome numbers may be expected, if different populations are examined.

Some verification of chromosome number relationships was sought in stomata number per sq. mm. This method was first suggested by K. and H. J. Sax (1937). Babcock and Stebbins (1938) used stomatal size as a criterion to indicate chromosome number in *Crepis*. In *Dentaria*, neither method proved to be completely satisfactory. However, in three species, *D. diphylla*, *D. laciniata*, and *D. maxima*, stomatal counts per sq. mm. could be used with some degree of accuracy. *D. diphylla* averaged 92 stomata, *D. laciniata* 52 stomata, and *D. maxima* 65 stomata per sq. mm. It was not possible to distinguish *D. heterophylla* and *D. multifida* by this technique.

STERILITY IN THE GENUS DENTARIA

Sterility in some European species, particularly *Dentaria bulbifera*, has been the subject of several papers, Ernst, (1918), Gams, (1922), Schwartzenbach, (1922), Leopold (1928), and Fritsch, (1922). Eames (1903) remarked on the sterility of *D. diphylla*, and the new edition of Gray's Manual notes that siliques are rarely matured in *D. diphylla* and *D. maxima*. While studying herbarium specimens, observation of those specimens that had fruiting material showed that although pods were developed, few, if any, developed mature seed. Studies in the field led to the same conclusion. Pods may develop to a good size, but when the contents are examined, they will most frequently be found to contain aborted ovules. Efforts to get apparently mature seeds of *D. diphylla*, *D. laciniata* and *D. maxima* from Ontario to germinate were entirely unsuccessful.

Causes of sterility were sought in pollen and ovules. Anthers of all species were observed for aborted pollen. In all, 70 specimens from throughout the area of the genus were examined, and with few exceptions the percentage of normal appearing pollen was high. Even in those specimens that were considered by the collector to be hybrids, good pollen was usually the rule. It was evident that sterility could not be attributed to poor pollen.

This led to the questions: Were the flowers being pollinated? Is self- or cross-pollination required for production of seeds? To obtain some answers to these questions 50 flowers from each of the species *D. diphylla*, *D. maxima*, and *D. laciniata* were self-pollinated, and 50 flowers of each were cross-pollinated with pollen from what were considered to be different clones. Not one seed was obtained from these pollinations. This would confirm observations that these three species are highly sterile.

Sections of ovules of the same three species were studied, and it was observed that shortly after the eight-celled stage was reached in the embryo sac, disintegration of the cells of the embryo sac took place and the ovules finally aborted and died. The eastern North American species of *Dentaria* proved to be another example of a polyploid series being sexually sterile. Undoubtedly they reproduce mostly, if not entirely, apomictically by vegetative reproduction, for which the nature of the rhizome seems admirably suited. In this respect they resemble *D. bulbifera* as discussed by Ernst (l.c.), *D. glandulosa* by Schulz (l.c.).

Discussion

This study of the eastern North American species of *Dentaria* indicates that there is great difficulty in determining the species by morphology alone. Numerous plants with intermediate characters appear and there is an intergradation of characters in most of the species. Cytological investigations indicate that the species in the area being considered have high polyploidy, $2n = 64, 96, 112, 128, 208$, and 240, and these numbers support the separation of the species. Normal pollen, with few exceptions, throughout the range of the genus is high. It has been found, in at least three species, that disintegration of the contents of the embryo sacs takes place shortly after they have reached the 8-celled stage. The same three species are sexually sterile and reproduce vegetatively by rapid development of the rhizomes, particularly in the early spring and during the time of flowering.

It is apparent that we have in this group of plants, an agamic complex similar to that described by Babcock and Stebbins (l.c.) in western American members of the genus *Crepis*. However, we have not yet discovered the diploid ancestors of this eastern North American complex. Probably they have been overlooked, or, they may no longer be in existence. As Stebbins (1941) has pointed out, "The systematic structure of an agamic complex can be understood only when its diploid sexual members are all known, and the limits of their variability have been determined." We are, therefore, compelled to discuss our representatives from the data that are available.

It is well known that in genera such as *Taraxacum*, *Hieracium*, and *Crepis* certain groups are highly polymorphic. This polymorphism may be attributed to hybridization, polyploidy, and apomixis. Stebbins (l.c.) has pictured the development of the agamic complex, and *Dentaria* seems to fit well into this picture. The diploid species, which were well defined systematically, by hybridization and polyploidy produced many new forms which because of their adaptability were able to invade habitats unsuited to their diploid parents. They may even have crowded out the diploid parents, if they ever existed on this continent. The numerous variations that were produced were finally reduced by the process of natural selection to the few remnants which represent our present species, and the many intermediates that cause so much taxonomic difficulty.

Gustafson (1947) showed that hybridization and polyploidy contribute to the production of apomicts. Hybridization may bring together genes responsible for sexual sterility, and polyploidy builds up the numbers of these genes, and may also alter the physiological condition of the cells so that the sterility factors may have full expression. In our highly polyploid members of the genus *Dentaria*, there has been a great accumulation of these sterility factors, and the genus has reached the stage of evolution where there is complete sexual sterility. The genus, therefore, depends for its existence on vegetative reproduction. According to Stebbins this is the last stage in the evolution of apomicts. Having lost their sexuality, they can produce nothing new and eventually die out.

The distribution of *Dentaria maxima* north of the southern limits of the glaciation is an interesting phytogeographical problem. That it is a hybrid between two of our species, *D. diphylla* and *D. laciniata,* as suggested by Wiegand and Eames, is excluded for several reasons. These two species are usually found in dry mesophytic woodlands, but *D. maxima* has been found most frequently in low, moist, wooded areas or on moist, wooded hillsides. The chromosome number, $2n = \pm 208$ does not indicate a hybrid origin with these two species as parents. The sexual sterility of *D. diphylla* and *D. laciniata* also argues against its being a direct hybrid between these two species; and for similar reasons it seems highly improbable that it can be a hybrid between any species of *Dentaria* now known in eastern America.

It would seem then, that *D. maxima* is a member of the agamic complex that originated before complete sexual sterility was effected in the members of the complex. It may have been derived during some interglacial period of the Pleistocene glaciation. During the Wisconsin glaciation the species survived near the border of the ice sheet, and with the return of temperate conditions found the glaciated soils a more suitable habitat than the Tertiary soils to the south.

Conclusions

1. The species of the genus *Dentaria* in eastern North America are highly polymorphic, and sharp morphological lines of distinction between species cannot be drawn.
2. The species *D. diphylla, D. multifida, D. heterophylla, D. maxima,* and *D. laciniata* can be distinguished cytologically on the basis of chromosome numbers. All species are high polyploids.
3. Sexual sterility is known to occur in three species, *D. diphylla, D. maxima* and *D. laciniata.* Examination of specimens of *D. heterophylla* and *D. multifida* indicates that sterility also occurs in these species. Sterility has been shown to be the result of incomplete development in the embryo sac.
4. The genus is considered to be of ancient origin, and the polymorphic character of the species is the result of hybridization, polyploidy and apomixis.

5. *Dentaria maxima* occurs only in the glaciated regions of eastern North America, and is thought to have originated during some interglacial period. After the Wisconsin glaciation it migrated north into the glaciated areas rather than south into the tertiary soils.

Key to the Eastern North American Species of Dentaria

- a. Rhizome not segmented or with alternately enlarged and slightly constricted regions; rachis glabrous (rarely pubescent).
  - b. Diameter of rhizome constant along its entire length; cauline leaves mostly 2, opposite or alternate; trichomes on margins of leaflets 0.1 mm. long and appressed . . . . *D. diphylla.*
  - b. Rhizome with alternately enlarged and slightly constricted regions; number of cauline leaves and arrangement variable but most frequently 3 and alternate; trichomes on margins of leaflets 0.2–0.3 mm. long and spreading . . . . *D. maxima.*
- a. Rhizome definitely formed of segments united by fragile connectives.
  - c. Rachis pubescent (rarely glabrous); trichomes of rachis and margins of leaflets 0.2–0.3 mm. long and spreading . . . . *D. laciniata.*
  - c. Rachis glabrous (rarely pubescent).
    - d. Cauline leaves usually 2, opposite or alternate; leaflets 3; trichomes on margins of leaflets 0.1 mm. long and appressed . . *D. heterophylla.*
    - d. Cauline leaves most frequently 2; leaflets dissected into 3–7 linear segments 1–3 mm. broad; margins of leaflets without trichomes . . . . *D. multifida.*

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